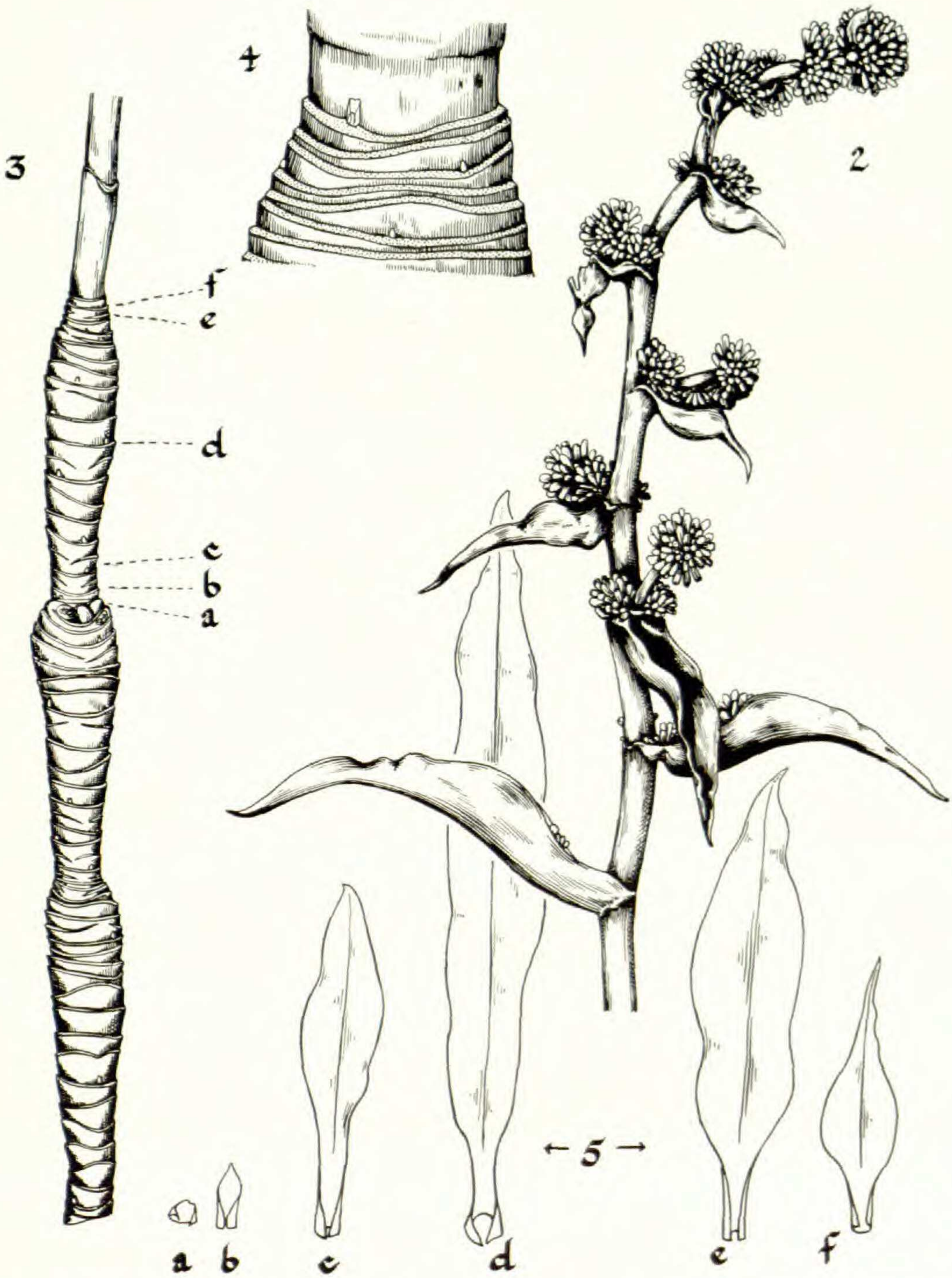
FIG. 1. *Dracaena fragrans*. Distal part of a flowering shoot, × 1/5.

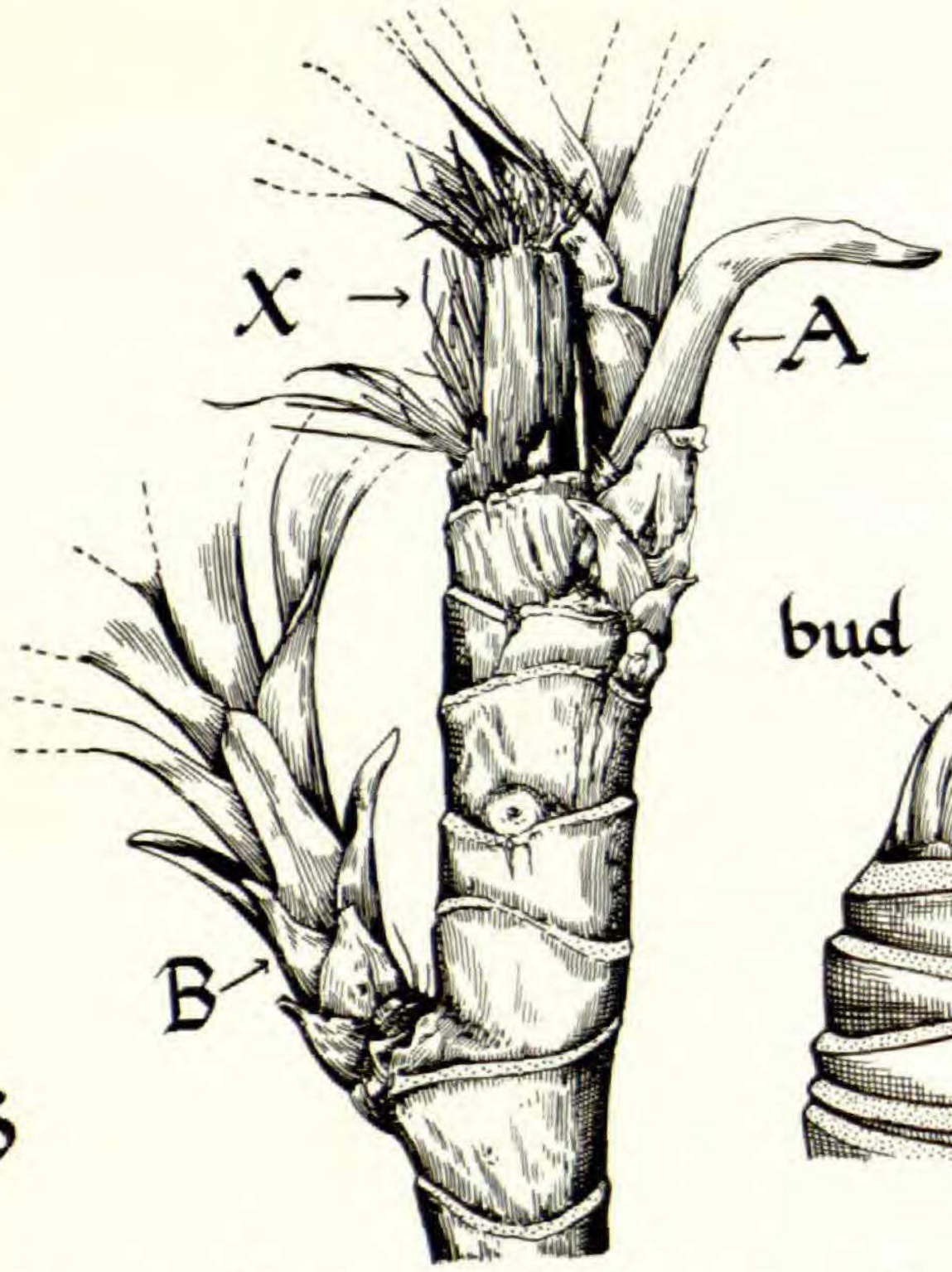
tion in leaf size associated with an abrupt elongation of internodes (FIGS. 2–5). Bracts which subtend the first-order flowering branches are white and caducous although it is obvious from the transition upwards along the shoot that they are homologous with foliage leaves. The detailed structure of the flower-bearing branches has been described by Troll (1962).

Branching is normally sympodial from a bud in the axil of one of the transitional leaves immediately below the inflorescence. At the time of anthesis this renewal bud is indistinguishable from other dormant buds (FIG. 4). After flowering it grows out rapidly (FIG. 7), pushing the terminal inflorescence into a pseudolateral position. Each axis branches in this way and is, therefore, a sympodium consisting of many successive growth units. The sympodium appears articulate both from the scars of the dried inflorescence stalks, and a swelling which marks each joint (FIG. 3). This articulation is most noticeable in distal, horizontal axes.

After flowering there is an evident competition among a number of potential renewal buds, because the inhibition of more than one is always released (FIG. 7). One of them usually becomes dominant and re-imposes inhibition upon the others. However, two (rarely more) buds may grow out simultaneously. This leads to a branched axis with an inflorescence scar in the crotch of the fork. Plants in South Florida flower several times in one year and although it is obvious that different axes flower at different times of the year it seems likely that a vigorous shoot can flower



FIGS. 2–5. *Dracaena fragrans*. Habit details. *2*, Terminal inflorescence, × 1/2. 3, Flowering shoot with all leaves detached, showing 3 units of sympodium and base of inflorescence axis as a continuation of vegetative axis, × 1/2. Letters indicate levels of insertion of corresponding leaves shown in FIG. 5. 4, Detail of region of transition from vegetative to reproductive axis, × 2, leaves removed at their insertion; buds shown in axils of a number of leaves. 5, Series of leaves (a–f) from distal unit shown in FIG. 3, their levels of insertion indicated in that figure, beginning with prophyll (a) and ending with most distal transitional leaf (f), × 1/4.



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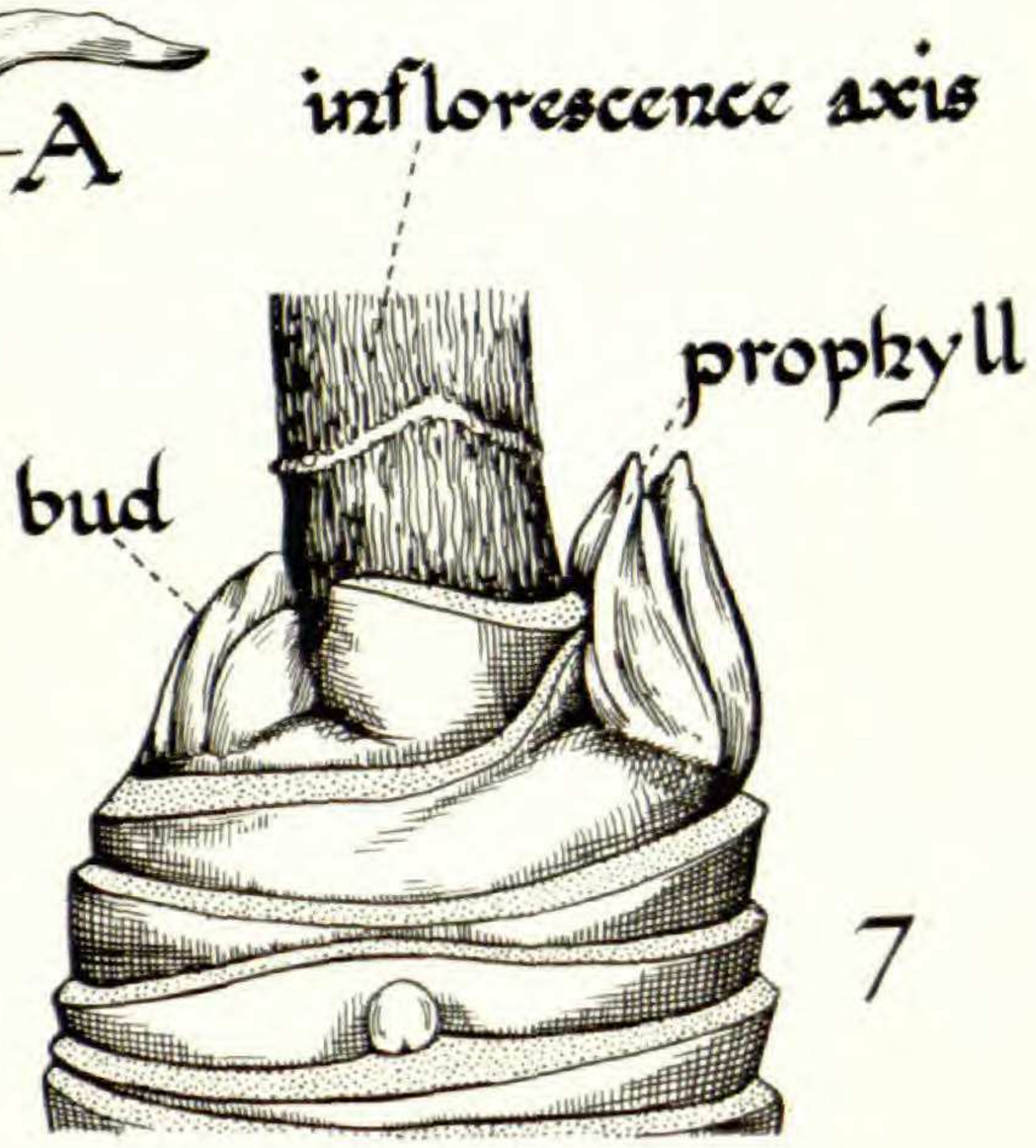

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FIGS. 6 and 7. *Dracaena fragrans*. Branching. 6, Erect axis with 2 branches, renewal shoots at A and B from axillary buds whose inhibition is released by destruction of apex of parent shoot at X, × 2/3. 7, Normal renewal growth below old inflorescence axis, × 2. Buds developing in axils of two most distal leaves; prophylls conspicuous. This corresponds to FIG. 4 after lapse of 2 months.

two or three times each year. This is indicated by a close succession of inflorescence scars. For a further morphological description of flowering in arborescent Liliiflorae the reader is referred to the detailed work of Schoute (1903, 1918).

The release of apical dominance is normally the result of flowering but it may be induced in other ways. Decapitation releases from inhibition the dormant buds immediately below the injury (FIG. 6). Apical dominance is also released on the upper side of leaning stems where numerous dormant buds may grow out, much as in woody dicotyledons (see *Fig. 15* in Tomlinson & Zimmermann, 1969). Erect, rapidly growing suckers commonly develop from the base of old plants, presumably for the same reason. The influence of these various methods of growth on the distribution of vascular tissue is largely described in the second article of this series.

Primary tissues (FIG. 8). Epidermis slightly thick-walled, covered by a thin but conspicuous cuticle. Periderm in hypodermal or subhypodermal layers developing early by etagen-like divisions of cortical cells, the outermost derivatives suberized. Cortex, 1–3 mm. wide, of uniform and fairly compact parenchyma; no independent cortical vascular system

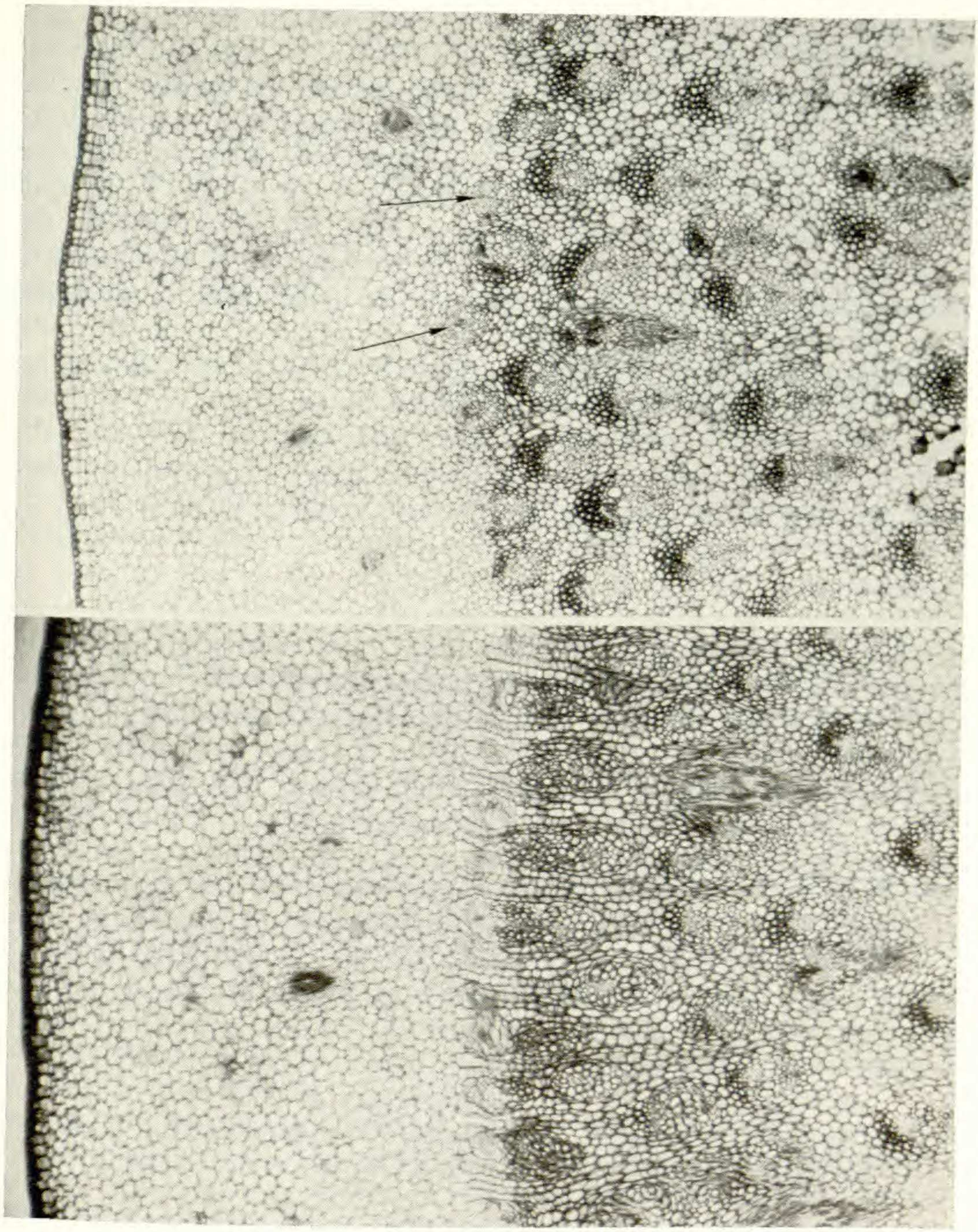

FIG. 8. (ABOVE). Transverse section of mature primary stem of *Dracaena fragrans*, × 36. All bundles in cortical area are leaf traces. Arrows point out vertical bundles immediately above point of branching from leaf trace. They appear small because they lack the fibrous sheath.

FIG. 9 (BELOW). Transverse section of mature stem of *Dracaena fragrans*, taken from the same stem, a few centimeters higher, below the sympodial branch. A small amount of secondary tissue has been formed by the cambium, × 36.

developed. Central cylinder delimited by compact, often lignified ground parenchyma and peripheral, congested vascular bundles. Central bundles more diffusely distributed among thin-walled ground tissue resembling

parenchyma of cortex. Vascular bundles each with a sheath of narrow compact angular cells, the sheathing cells thick-walled around phloem but sheath becoming more uniformly sclerotic around peripheral bundles. Vascular tissues collateral, including a wide strand of angular metaxylem elements, V-shaped in transverse section, usually with narrow protoxylem elements at the apex of the V and a single phloem strand in the angle of the V. Peripheral vascular bundles with little or no protoxylem, the metaxylem scarcely V-shaped. Leaf traces conspicuous in outer part of central cylinder, the xylem represented largely by abundant protoxylem. Xylem including fairly wide angular tracheids with indistinct end walls and scalariform pitting. Protoxylem elements rounded, with annular or spiral wall thickening. Metaxylem tracheids of the order of 5–10 mm. long, and overlapping extensively. Phloem including long sieve-tube elements usually with transverse end walls and simple sieve plates, but sieve plates commonly compound on oblique or very oblique end walls. Raphide clusters common in otherwise unmodified parenchyma cells. Tannin cells infrequent.

Secondary tissues (FIG. 9). This arises from an etagen cambium of the type which has already been described in the earlier review (Tomlinson & Zimmermann, 1969). Ground tissue of compact tabular and radially-arranged cells about 120μ long, with slightly thickened and lignified cells, the walls with abundant simple pits. Tannin deposits and raphide clusters frequent. Secondary vascular bundles always amphivasal. Central phloem strand including short sieve-tube elements with simple, more or less transverse sieve plates. Phloem separated from xylem by short, thin-walled parenchyma cells. Secondary tracheids conspicuously different from those of primary vascular bundles; of the order of 3.6 mm. long and with indefinite end walls; walls thick; bordered pits with crossed slit-like apertures, more or less parallel to the axis of the cell. Short xylem parenchyma cells infrequent.

The difference in length between secondary ground tissue cells and secondary tracheids suggests that the latter undergo about a 30-fold extension during development since both arise from similar initials.

COURSE OF PRIMARY VASCULAR BUNDLES

The distribution of primary vascular tissue in *Dracaena fragrans* is similar to that of the palm *Rhapis excelsa* as described by us (Zimmermann & Tomlinson, 1965) with slight quantitative differences. Each leaf is supplied with a number of leaf traces which diverge from the stem at varying depths. Major bundles diverge from the center, minor bundles from near the periphery, and intermediate bundles from an intermediate area of the stem. Outgoing leaf traces produce a number of derivative bundles by branching. Most of these branches are short bridges which link in an upward direction with nearby vertical bundles. Axial continuity from each leaf trace is maintained by a continuing vertical bundle which

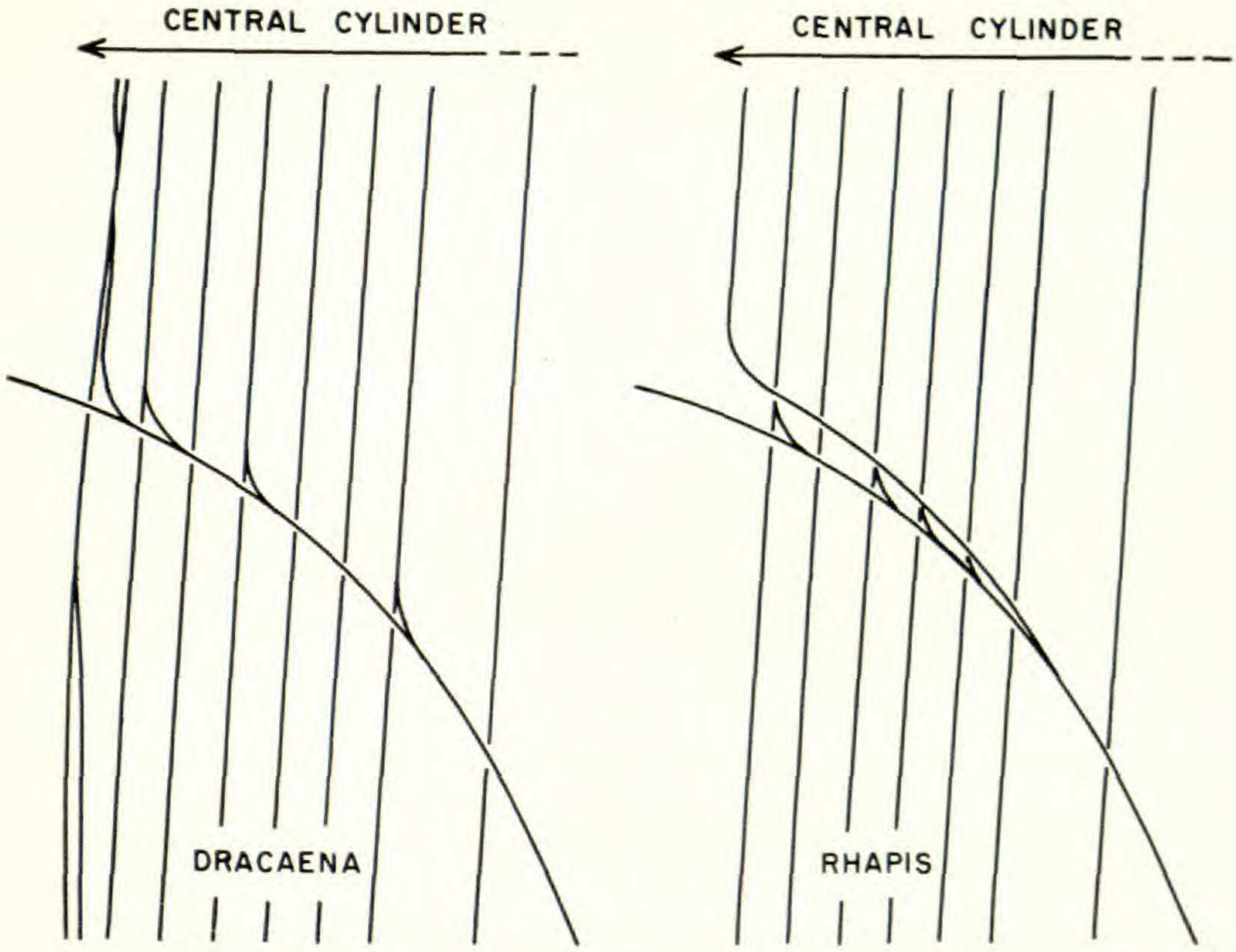

FIG. 10. Diagrammatic representation of leaf-trace departure in *Dracaena fragrans* (LEFT) and *Rhapis excelsa* (RIGHT). In *Rhapis* the vertical bundle is usually the lower- and innermost branch of the leaf trace. From the point of branching it follows the leaf trace to the periphery of the central cylinder. In *Dracaena*, the vertical bundle usually branches from the leaf trace outside and above the bridges. Newly released vertical bundles show a tendency to anastomose among themselves. For an unusual type of vertical-bundle branch see TEXT and FIG. 13.

usually diverges from the leaf trace at the very periphery of the central cylinder. The newly released vertical bundle is normally very narrow if the stem does not contain secondary tissue (FIG. 8). In this very peripheral position it readily splits or anastomoses with similar neighboring bundles on its way up the stem. This contrasts with the situation in *Rhapis* where the vertical bundle is released near the stem center and accompanies the parent leaf trace, on its outwardly diverging path, almost all the way to the periphery of the central cylinder (FIG. 10). The upwardly continuing vertical bundle, as in *Rhapis*, then gradually approaches, over a distance of many internodes, the center of the stem whereupon the process of bundle branching is repeated again in association with another, more distal leaf. Major bundles have the longest, minor bundles the shortest distances between two such successive leaf contacts. Thus, the overall course of vascular bundles is similar to that illustrated for *Rhapis* (Zimmermann & Tomlinson, 1965; *Fig. 3*, right). In *Dracaena*, in contrast with *Rhapis*, the central bundles have no helical path. Major dorsal bundles merely describe a turn of about 120° in the center, as described

in the next section of this paper. This turn, as with the helical twisting in *Rhapis*, is in the direction of the phyllotactic spiral. This turn may be governed by the same developmental principle which causes phyllotaxis.

The distribution of protoxylem changes throughout each bundle in the same manner as in *Rhapis*. This change is less conspicuous in *Dracaena* than in *Rhapis* because protoxylem and metaxylem elements are more nearly of the same diameter. As one follows a vascular bundle of *Dracaena* in a distal direction one finds protoxylem first not very far above its divergence from the leaf trace as a vertical bundle. Continuing upwards, the number of elements further increases to reach a maximum where the bundle passes out into another leaf. Metaxylem is continuous into bridges as well as the continuing vertical bundle but the leaf trace contains only protoxylem. In this respect *Dracaena* is identical with *Rhapis* although the "loss" of metaxylem from the outgoing leaf trace is less obvious because the two tissues are not so clearly distinguished.

Irregularities in the course of bundles throughout the stem are somewhat more common than in *Rhapis*. The anastomosing tendency of the lower part of vertical bundles, at the periphery of the central cylinder, has been mentioned. If the stem consists of primary vascular tissue only, the vertical bundles are quite small in their lowermost portion, at the periphery, where they come off the leaf trace and without a well-developed fibrous sheath (FIG. 8). In places where the primary vascular cylinder is covered by a mantle of secondary tissue, the same vertical bundles are larger and more conspicuous, because the fibrous sheath is better developed (FIG. 9).

Another irregularity which has been observed is the occasional forking leaf traces. When such a bundle is followed upwards in the stem center, the two branches diverge along two different radii. From these observations it appears that developmental processes are somewhat less rigid in *Dracaena* than in *Rhapis*.

The important topic of the relation between primary and secondary vascular bundles is reserved for the second article in this series.

DEVELOPMENTAL PATTERN OF THE PRIMARY VASCULAR SYSTEM

Observations. General aspects of the anatomy of the meristematic crown are shown in the photomicrographs, FIGURES 11 and 12. Leaves and leaf primordia are arranged in a phyllotactic spiral with a divergence between 1/3 and 2/5, as can be seen from FIGURE 11. The approximately median longitudinal section through the crown shows the usual monocotyledonous organization (FIG. 12). It is obvious from this longitudinal section that primary thickening growth involves re-orientation of tissue through about 90° as we have described for *Rhapis* and *Prionium* (Zimmermann & Tomlinson, 1967, 1968).

The developing vascular system of the meristematic crown is far too complex to be demonstrated in individual microtome sections. Provascular strands were, therefore, followed throughout a series of transverse sections and their radial distance from the stem center plotted on graph paper as

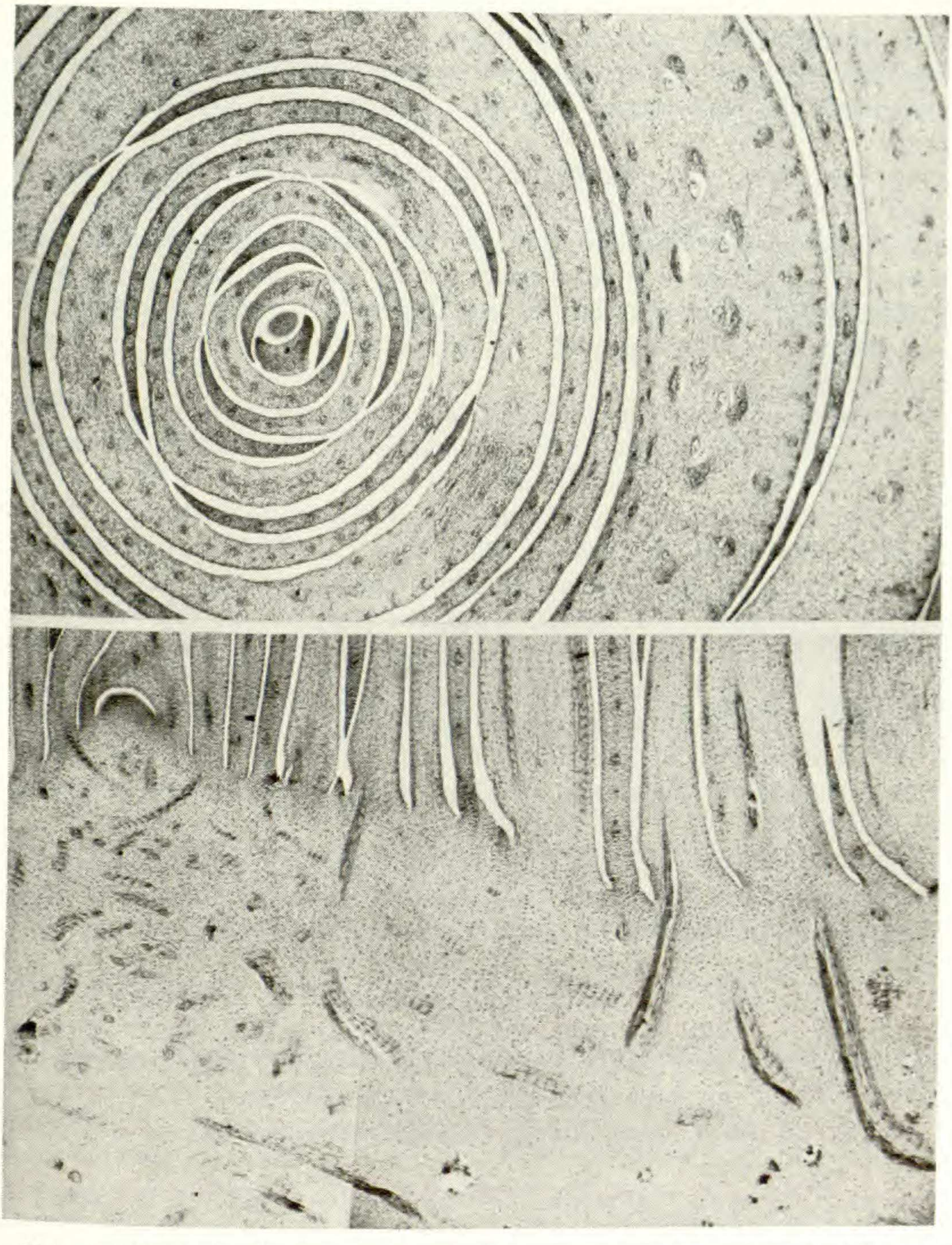

FIG. 11 (ABOVE). Photomicrograph of transverse section through the meristematic crown of *Dracaena fragrans* at the level of the apical meristem, × 26, showing the phyllotactic arrangements of the leaves. Note the symmetrical arrangement of the major leaf traces on the dorsal side.

FIG. 12 (BELOW). Approximate median longitudinal section through the meristematic crown of *Dracaena fragrans*, × 26. Because of their complex three-dimensional path, none of the individual provascular strands can be seen over more than a very short distance. A thorough knowledge of their path, gained through plotting (FIG. 13 and TEXT) enables us to interpret a single section like this quite easily. Note the sharp turns of the major strands below the apical meristem. Note also the minor leaf trace on the far right of the photograph.

had been done for *Rhapis* and *Prionium*. The results are shown in FIGURE 13. The three-dimensional arrangement of provascular strands in the crown is difficult to represent on paper, our representation is therefore simplified as follows. All radii are shown in a single plane. All leaves are rotated into the same plane. This eliminates the 120° turn of the major bundles. In order to reconstruct the three-dimensional pattern of the crown from FIGURE 13, the reader has to go through a mental exercise which first involves rotating leaves back to their proper position, and second involves re-establishing the 120° turn of the major bundles. This process of simplification is very similar to the one used in our description of the *Rhapis* crown. It has the advantage that one can more easily appreciate the re-orientation of a major dorsal bundle during successive developmental stages.

FIGURE 13 shows the major dorsal leaf trace in leaf primordia P 1 to P 17, P 1 being the youngest visible primordium. The pattern of vascular development appears to be the same as the one found in *Rhapis* and *Prionium*. Vertical bundles originate from major leaf traces of P 17. Approximately below the base of P 14 they fuse into the meristematic cap into which all blind-ending vertical bundles converge (cf. Zimmermann & Tomlinson, 1967, 1968). From the diagram one can extrapolate that the leaf-contact distance for a major bundle is about 20 to 25 internodes, although the series of sections was too short to show this directly. If the section series had been longer and had included the insertions of older (lower) leaves, the major leaf trace of P 1 would have been seen originating as a vertical bundle from a leaf trace diverging into a leaf at about the level of P 20–25.

A rather unusual type of vertical-bundle branch was found in two major leaf traces to P 11. Both vertical bundles ended distally immediately below the apical meristem in what might be a leaf primordium younger than P 1 and represented by an indistinct ridge. If this interpretation is correct there would be a leaf-contact distance of 11 internodes between P 0 and P 11. Only two such centrally located vertical bundle branches were found and one of them is shown in FIGURE 13. The developmental meaning of this rare type of vertical bundle is unknown.

FIGURE 13 shows some further irregularities which are of no fundamental significance, such as the apparent crossing over of the lower portions of the major leaf traces of P 1 and P 2, P 5 and P 6, P 7 and P 8. They could have resulted by comparing bundles on different radii of the stem (the crown is not perfectly circular in transverse section), from slight irregularities of development, or indeed, from the process of plotting.

The meristematic cap is similar in position and extent to that described in the apices of *Rhapis* and *Prionium*. It is recognized as the umbrella-shaped meristematic area, below the shoot apex proper, into the periphery of which the blind-ending vertical bundles fuse. It is pierced by leaf traces already connected to vertical bundles.

The primary vascular connection between an axillary bud and the vascular system of the central cylinder has also been traced in this series

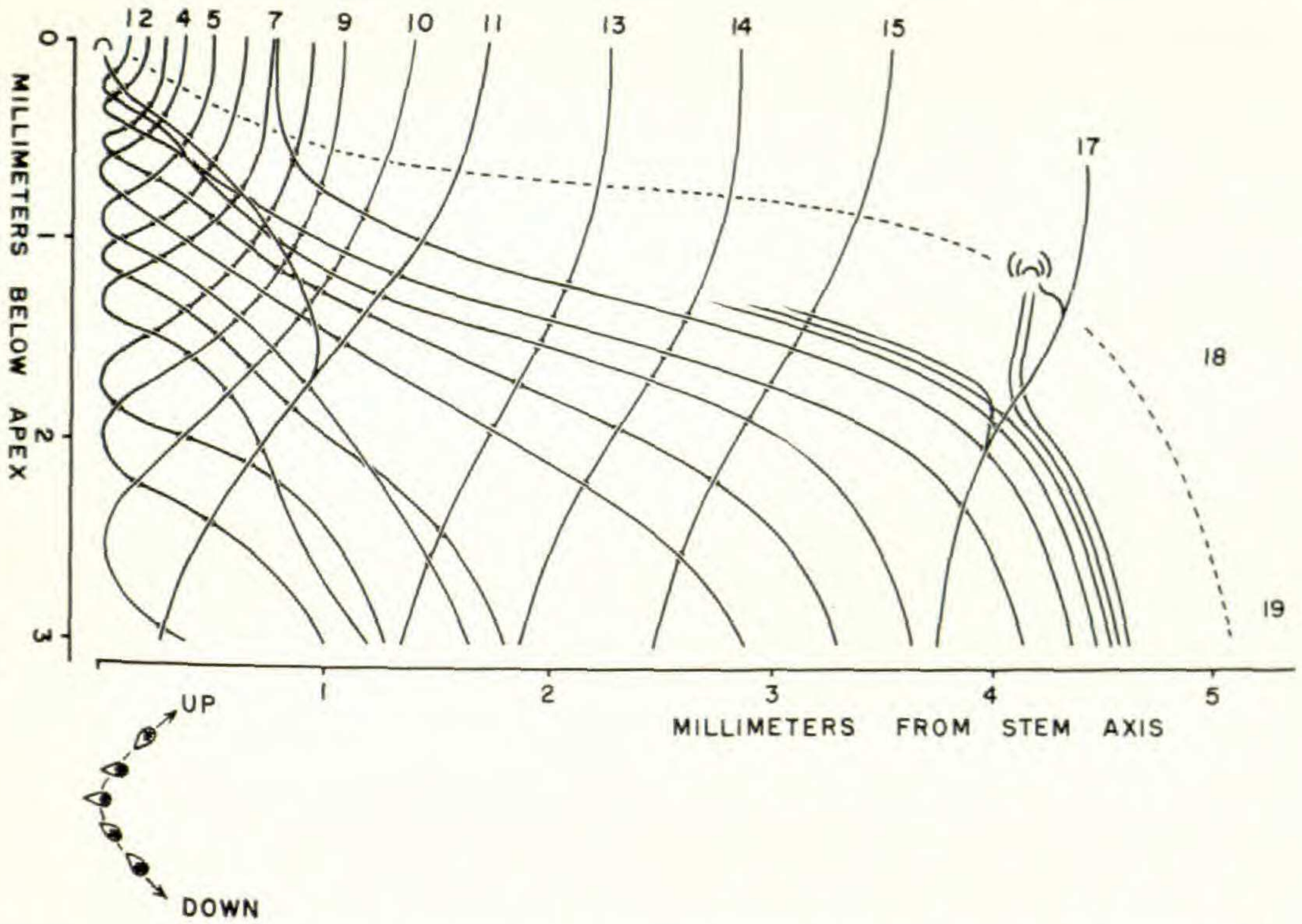

FIG. 13. The path of major leaf traces from leaf primordia 1 through 17, obtained from plotting each individual bundle through a series of transverse sections. In this diagram, all radial distances are plotted within a single radial plane regardless of position in the third dimension. The diagram therefore does not represent a real radial section as in FIG. 12. Major leaf traces P 1 to P 17 are shown, for P 7 also a minor one. The reader has to visualize that there are numerous intermediate leaf traces between these two extremes, from each leaf. Vertical bundle branches normally appear from leaf traces of P 17. The one shown from leaf trace P 11 appeared unusually early (see text). Vascularization of the axillary bud of P 17 includes two vertical bundles and one satellite bundle. The dashed line marks the approximate level of leaf insertion. INSET BELOW. The 120° turn of the major leaf traces in the stem center, as seen in successive transverse sections.

of sections. The provascular connection between axillary bud and stem was established only in P 17 and older leaves. In P 15 the axillary bud meristem was apparent but still entirely without discernible procambial strands. This suggests that vascular continuity between axillary buds and main axis is established late, in the manner of minor leaf traces. A more detailed discussion of the development of the vascular system of axillary buds will follow in the second paper of this series.

Developmental inferences. The sequence of vascular development is thought to be as follows. Leaf traces link up with a potential vertical bundle in the cap, then differentiate out below the cap. Leaf traces which develop early, i.e., those arising in a position near the center of the cap, become major bundles; those developing further out, near the cap periphery, become minor bundles. For comparison both a major and a minor trace from P 7 are shown in FIGURE 13.

These developmental processes have been discussed in detail in our articles on the developmental pattern of the vascular system of *Rhapis* and *Prionium*. We may merely point out here that there are no cortical bundles in *Dracaena*, a fact which is of utmost significance as we shall see in the next paper of this series.

DISCUSSION

In a previous review (Tomlinson & Zimmermann, 1969) we have noted that von Mohl (1824) equated the primary vascular system of "*Aletris fragrans*" and other species which he studied with that of a palm, in so far as he understood the course of vascular bundles in the palm stem. Von Mohl's contemporaries and all subsequent investigators who studied arborescent Liliiflorae at first hand claim to have confirmed his observations (e.g. Meneghini, 1836; Millardet, 1865; de Cordemoy, 1894; and others). However, our own more recent investigation of the palm stem (Zimmermann & Tomlinson, 1965) has shown that von Mohl's understanding was incomplete, because he overlooked the axial continuity of vascular bundles which is so important in long-distance transport. We have already given our historical interpretation of the topic (Tomlinson & Zimmermann, 1966) and need not discuss it any further. The present study of *Dracaena fragrans* has confirmed that von Mohl was right in principle. The primary vascular anatomy of the axis of this plant does indeed correspond in all essentials with that of a palm, but we now have a much more complete understanding of the anatomy of the palm and its development. *Dracaena* conforms in the pattern of primary vascular differentiation, a pattern which we believe is fundamental for monocotyledons as a whole (Zimmermann & Tomlinson, 1965, 1967, 1968).

Our cinematographic analyses have included other species and genera of arborescent Liliiflorae. Analysis of the mature axis of *Cordyline terminalis*, *Dracaena marginata* and *Pleomele* (*Dracaena*) *reflexa* confirms the course of vascular bundles described for *Dracaena fragrans*. Single sections which we have prepared from the stems of several other genera and species can also be interpreted according to our three-dimensional analysis. This additional evidence puts our interpretation on firm ground.

SUMMARY

The primary vascular system of arborescent Liliiflorae was thought by von Mohl and subsequent investigators to be equivalent in principle to that of palms. An analysis of the system in the vegetative axis of *Dracaena fragrans* with the aid of cinematographic methods confirms this. In addition, however, it also shows that axial continuity of the palm type, overlooked by these early anatomists, which has only recently been demonstrated, also occurs in *Dracaena* and related plants. The origin of the primary vascular system has been traced by plotting the course of provascular strands in the developing crown. We regard, on the basis of

similar studies of other plants, this pattern as fundamental for the monocotyledons. The basis has thus been laid for a future investigation of secondary vascular tissues in these plants.

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COMPARATIVE MORPHOLOGICAL STUDIES IN DILLENIACEAE, IV. ANATOMY OF THE NODE AND VASCULARIZATION OF THE LEAF

WILLIAM C. DICKISON

IN A CONTINUING EFFORT to provide comprehensive anatomical information which might prove useful in elucidating taxonomic and phylogenetic relationships of the Dilleniaceae, an extensive investigation of nodal and leaf vasculature was undertaken.

Aside from remarks pertaining to ovular structure by Cordemoy (1859), and an occasional reference to internal structure by various other workers, the earliest comprehensive anatomical investigations on Dilleniaceae are the contributions of Baillon (1866–67, 1871) and Hitzemann (1886, cited by Ozenda, 1949).

The first comparative morphological studies on the family to appear were those of Parmentier (1896), who found the leaf to contain characters of diagnostic value, and Steppuhn (1895) who made an extensive investigation of stem, leaf, and root of some one hundred fifty dilleniaceous species.

Solereder (1908) and Metcalfe and Chalk (1950) published additional anatomical information, but contributed little to help clarify the phylogenetic position of the group. The most recent study on comparative vegetative anatomy of the family was by Ozenda (1949) whose observations on seedling, nodal, and leaf anatomy were scattered among seven genera.

All researches referring to the Dilleniaceae, therefore, are either incomplete, or else were produced in the last century and thus warrant reinvestigation. This paper describes heretofore unreported anatomical data of both taxonomic and phylogenetic significance.

MATERIALS AND METHODS

Material of over one hundred dilleniaceous species was examined. Specimens studied were received from, or are housed in: the Arnold Arboretum, Harvard University (A); State Herbarium of South Australia, Adelaide (AD); Arizona State University, Tempe (ASU); Botanic Museum and Herbarium, Brisbane (BRI); Commonwealth Scientific and Industrial Research Organization, Canberra (CANB); Royal Botanic Garden, Edinburgh (E); Gray Herbarium, Harvard University (GH); Royal Botanic Gardens, Kew (K); Botanical Survey of India, Southern Circle, Coimbatore (MH); Missouri Botanical Garden, St. Louis (MO); Animal Industry Branch, Northern Territory Administration, Alice Springs (NT); Western Australian

Herbarium, Perth (PERTH); Rancho Santa Ana Botanic Garden, Claremont (RSA); Sarawak Museum, Kuching (SAR); Botanic Gardens, Singapore (SING); University of California, Berkeley (UC); and the United States National Museum, Washington (US). The assistance of the curators of these collections is gratefully acknowledged. I also wish to thank Doctors R. D. Hoogland, H. Keng, and C. R. Metcalfe for providing seed used in this study.

The study of lamina vascularization was accomplished entirely through the use of cleared leaves. Clearing was carried out using the standard NaOH method followed by safranin stain. Dried materials were initially re-expanded in 5 percent NaOH prior to fixation and sectioning. Nodes were serially sectioned and stained with a combination of safranin-fast green. Petiole vasculature was followed by obtaining sections throughout the length of the petiole as well as midway through the midrib.

NODAL ANATOMY

No detailed, comprehensive study of nodal anatomy in the Dilleniaceae has previously been undertaken. Sinnott (1914) attempted to utilize the nodes of several genera within the family (*sensu* Gilg, 1893) as evidence to support his idea that the trilacunar node was primitive; furthermore, that the unilacunar and multilacunar node was derived by reduction or amplification. This author listed six genera of the Dilleniaceae (*sensu stricto*) as having tri- or pentalacunar nodes.

Ozenda (1949) after an examination of *Hibbertia, Dillenia, Schumacheria, Tetracera, Curatella,* and *Davilla* also concluded that the mature nodes of the family were tri- or multilacunar; however, he was of the opinion that the multilacunar condition was the primitive pattern. The primitive nature of the multilacunar node in the Dilleniaceae has also been advocated by Meeuse (1966, p. 49).

As a result of comparative morphological data from both fossil and extant plants, in addition to ontogenetic considerations, the primitive nature of the trilacunar node was questioned by Marsden and Bailey (1955) and Canright (1955). These authors suggested that the unilacunar two-trace system represented the primitive condition. The unilacunar two-trace node is characteristically described as having two vascular traces which arise from independent primary bundles and, therefore, do not represent the dichotomy of a single median trace.

Pant and Mehra (1964) re-evaluated nodal anatomy in many Pteropsida, and concluded that the statements of Marsden and Bailey (*loc. cit.*) concerning nodal patterns in fossil ferns and gymnosperms were not always substantiated. They then advised caution in accepting the unilacunar two-trace node as primitive for all Pteropsida. Results from a study of developmental patterns in stem primary xylem indicated to Benzing (1967a, b) that the odd-numbered trace, unilacunar one-trace or trilacunar, was more likely to be primitive in angiosperms. A recent paper by Namboodiri and